FOREST BIRD COMMUNITIES IN THE APOSTLE ISLANDS OF WISCONSIN

BY EDWARD BEALS

In the past few years more ecologists have become aware that the description of plant and animal communities as discrete ecological units is an oversimplification of community relationships. Among botanists, Gleason (1926) has proposed that, inasmuch as each plant species has environmental requirements different from those of every other species, the classification of plant communities into separate and distinct associations is inadequate. Following this individualistic concept, many phytosociologists have developed vegetational gradients based either on measurement of environmental factors (e.g., Ramensky, 1930; Whittaker, 1956) or on a direct analysis of the vegetation itself (e.g., Curtis and McIntosh, 1951; Brown and Curtis, 1952; Goodall, 1954; Horikawa and Okutomi, 1955; Bray and Curtis, 1957). Animal ecologists have also used community gradients in studies of insects (Whittaker, 1952; Kato *et al.*, 1955), copepods (Whittaker and Fairbanks, 1958), and birds (Bond, 1957).

Because different bird species seldom if ever coincide in their ecological distributions, no discrete communities can be clearly defined except where there are sharp changes of environment. Therefore the present paper describes the bird populations within the forests of the Apostle Islands in Lake Superior in terms of a community gradient, relating these bird communities to their environmental framework. Scientific names of plants follow Gleason (1952).

Acknowledgments

I wish to acknowledge with gratitude the financial aid received from the Frank M. Chapman Memorial Fund, with which the project was completed. Part of the field work was accomplished while I was working on a vegetational survey of the islands for the Wisconsin Conservation Department, and the cooperation from the Department at the Bayfield station is appreciated. Appreciation is expressed also to Edward Nourse and Laurie Nourse, Jr., for helping with transportation problems. Special thanks are given Professor J. T. Emlen, Jr., for his encouragement and advice throughout this study, and to Professors Grant Cottam, J. T. Curtis, and J. C. Neess, for their valuable suggestions and critical reading of this manuscript.

Description of the Region

The Apostle Islands are situated in Lake Superior at the northernmost tip of Wisconsin. There are 22 islands in the group, most of which are low, rising no more than 50 to 75 feet above the lake level. Oak Island is an exception, rising nearly 500 feet. In size they range from a few acres to over 20 square miles. The largest, Madeline, has been most subjected to human disturbance, and it is the only island that supports a year-round human population. Several others have summer cabins.

The summer climate is remarkably cool, with a mean July temperature of 65°F. It is characterized by a high proportion of rainy days.

The islands lie in the hemlock–white pine–northern hardwoods region of Braun (1950). Extensive trembling aspen (*Populus tremuloides*) and white birch (*Betula papyrifera*) forests occur on some of the islands, where fire or logging has destroyed the original vegetation. Only a few forests of red, white, and jack pines (*Pinus resinosa, P. strobus*, and *P. banksiana*) occur on the islands. Red oak (*Quercus rubra*) forests may occur on higher locations. The predominant undisturbed vegetation consists of one or more of the following tree species: sugar maple (*Acer saccharum*), yellow birch (*Betula lutea*), white cedar (*Thuja occidentalis*), and hemlock (*Tsuga canadensis*). Dense populations of white-tailed deer (*Odocoileus virginianus*) have had a profound effect on the vegetation on some islands; elsewhere deer do not occur at all. Fields have been cleared on Madeline and Sand islands, and open bogs occur spottily, but the bird populations of these particular vegetation types were not studied in detail. For a general descriptive account of the birds of this region in all habitats see Beals (1958*a*).

Field Methods

In comparing communities it is desirable to study as many of them as possible in order to obtain more adequate information regarding the differences among communities. Therefore a rapid sample count method was used to census the birds in this study, somewhat similar to the methods used by Dambach and Good (1940) and by Bond (1957).

The sites were selected on the basis of previous studies of the vegetation (Beals, 1958*b*). Since much of the forested land is continuous on the islands, distinct stands of vegetation were seldom found. Areas of 20 to 40 acres, homogeneous in their vegetation at least for the dominant trees (Beals, 1958*b*), were selected for the vegetational survey. These stands had indistinct boundaries, except when bordering the lake, a bog, or a clearing.

The bird poplations of 24 stands were sampled in late June and early July of 1957 and in late June of 1958. The breeding season apparently reaches a peak around the end of June. Stands were usually sampled between five and eight o'clock in the morning, but on chilly mornings birds were active until nine or later.

A sample count was made by entering a given stand for about 100 yards, standing at a point for five minutes, recording the number and kinds of birds heard or seen, and then proceeding to another point within the stand 150 paces away (125 to 135 yards) and standing for another five minutes. This was repeated until ten points in the stand had been sampled. Birds seen flying high overhead, such as ducks and gulls, were not counted; those flying close to the canopy if not in it, including Chimney Swifts, Blue Jays, Common Ravens, Common Crows, and Cedar Waxwings, were included.

For each species, frequency (the number of points at which the species was observed) and density (the total number of individuals observed) were recorded in all the stands sampled. For loud-voiced birds or wanderers the same individual may have been observed at more than one point, so that frequency could have a higher value than density. An attempt was made not to count the same individual twice in the recording of density.

A method similar to this one has been checked for its accuracy in southern Wisconsin by Bond (1957), and he considered it a reasonable estimate of the relative values of bird populations. In this study one stand was sampled three times within one week, and the lowest similarity between any two of the samples was 84.9 per cent. (The method of calculating this similarity is described later.) This suggests that results from the sample count method are fairly constant. If one assumes that individuals of a given species of bird act similarly in different stands, in respect to their singing behavior and motor activity, the sampling method used here appears to be valid for a comparative study such as this one.

The sampling of a stand by this method took between one and one and one-half hours, so that if stands were close together, two could be sampled in a morning. However, most stands were rather far apart, and the mode of transportation (by foot or by boat) was slow, so that usually only one stand was sampled in a day.

Statistical Methods

Data from the field include two values for each species in each stand—the frequency and the density described above. These data are considered comparable for a given species between stands, assuming that the species does not differ appreciably in its conspicuousness from stand to stand. But comparisons between species within a given stand were made very cautiously, since species do differ markedly in their conspicuousness. Proportion of time spent singing, loudness of song or call notes, and amount of motor activity, all affect the observations recorded by the sample-count method. The density figure obtained by this sampling method might be distinguished from absolute and relative density figures as an "audiovisual" density index, which is presumed to bear some relationship to the absolute density for each species. Colquhoun (1941) developed coefficients of relative conspicuousness for various European species, which could theoretically be used in estimates of actual density. However, no valid estimate of the number of birds per fixed unit area is possible in this study, since no such "conspicuousness" coefficients are known and since the area of each sample is indeterminate. I have assumed that an estimate of absolute density is not necessary for comparisons of communities in the manner described below.

A single quantitative value for each species was desired in order to make comparisons between stands, and yet both frequency and density were considered necessary in determining the importance of the species in the community. Several birds observed at one point are considered less important, for example, than the same number of birds scattered throughout the community. The measure of such "importance" used by Bond (1957) was the sum of relative frequency and relative density. However, reducing frequency and density to relative values is not entirely satisfactory since direct comparisons were desired between stands for each species.

An index was obtained by multiplying the density of a species by the square root of its frequency, the product being called a "prominence value." It is to be distinguished from the "importance value," a term which has been used by plant and animal ecologists (Curtis and McIntosh, 1951; Brown and Curtis, 1952; Bond, 1957; and Beals, 1958*b*) to refer to a summation of relative figures, giving a constant value for the sum of all importance values in a stand. The term was first used by Curtis and McIntosh (1951) to denote the sum of relative frequency, relative density, and relative dominance of a tree species.

In determining the prominence value the number of individuals of a species in a stand is the most important figure, while the frequency, a measure of the distribution through the woods, is used to modify the density figure. The square root of the frequency is considered a sufficient modification, so that ten birds found all at one point are about one third as "prominent" as one bird found at each of ten points. By this method also, one bird observed at one point is half as "prominent" as one bird observed at four points. The index admittedly is arbitrary, but it is considered a reasonable quantitative method for describing the prominence of a species in a community.

A two-dimensional ordination of communities was constructed in a manner similar to that described by Bray and Curtis (1957) for plants. The method is based on a coefficient of similarity, calculated as $C = \frac{2w}{a + b}$, where a is the sum of quantitative values (in this case prominence values) of all species in one stand, b is the sum of quantitative values in another stand, and w is the sum of quantitative values the two stands have in common for each species.

To give a simple, hypothetical case, two stands have three species of birds: Stand A has prominence values for species X of 10, for species Y of 63, for species Z of 1; stand B has prominence values for species X of 1, for species Y of 33, for species Z of 36. To find w, the lowest values between two stands for each species are summed: $w = 1 + 33 + 1 = 35$. Therefore $C = \frac{2 \times 35}{74 + 70} = .486$; Stands A and B have a similarity of 48.6 per cent. The index ranges from zero, if the stands have no species in common, to 1.00 if they are by chance identical—exactly the same species in exactly the same amounts.

Birds with a high prominence value were more important in determining the coefficient of similarity than birds of low prominence. This procedure does involve the weighting of species within a stand; however, this weighting of prominence values no longer implies a comparison of density of birds within the stand. Prominence values were not reduced to relative figures (with a constant sum of 100 per cent) since this might obscure differences between stands for a given species, if the sum of prominence values was very different for the two stands.

A matrix was constructed showing coefficients of similarity for each of the stands with the 23 other stands. The coefficients were totaled for each stand, and the stand with the lowest sum could be considered the stand most different from all the others. It was used as one end of the first or x axis of the ordination. The other end stand of this axis was the stand having the least in common with the first.

Since this ordination attempts to arrange the stands according to their relative dissimilarity, inverse values of the coefficients of similarity were used, subtracting the coefficient from .85. This value was chosen rather than 1.00 because in sampling one stand three times, the coefficients of similarity between the samples were .849, .863, and .907. In other words, two stands with a similarity of .85 or higher should probably be considered essentially identical. Two stands with nothing in common would be 85 units apart (multiplying the inverse by 100). Expressed in these units, the distances between stands will be called *dissimilarity* values.

The length of the axis of an ordination is equal to the dissimilarity of the two reference stands. Each of the other stands is located by drawing arcs representing the dissimilarities from the two ends (Fig. 1). These arcs intersect each other above and below a line drawn between the two reference stands, and the arc intersection is projected onto this axis (Bray and Curtis, 1957). In practice the values of stands along an axis were calculated from a formula derived as follows. Two triangles can be found in Fig. 1, with sides exD_a and $e(L{-}x)D_b$, respectively. The hypotenuses are known (dissimilarities from the end stands, D_a and D_b); one side is equal in both triangles (the distance from the axis line to the arc intersection, e); and the sum of the third sides of the two triangles is known (the length of the axis, L). The triangles have the fol-

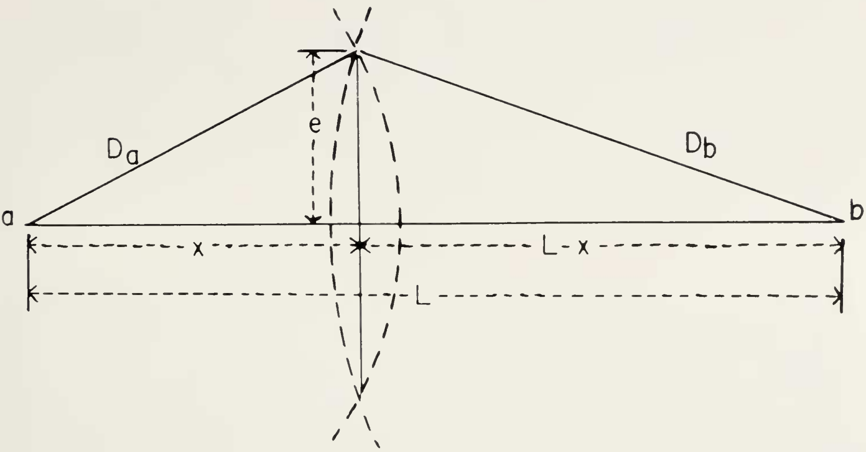

FIG. 1. Demonstration of stand location along an axis of the ordination, by projection of the point of arc intersection; a and b are reference stands, L is the dissimilarity value between the reference stands (the length of the axis), D_a and D_b are dissimilarity values of a given stand from the two reference stands, and x is the location of that stand along the axis.

lowing equations according to the Pythagorean theorem:

$$e^2 + x^2 = D_a^2$$

$$e^2 + (L-x)^2 = D_b^2$$

Subtracting one equation from the other, to eliminate e^2, and solving for x (the value along the axis from Stand A), the working formula results:

$$x = \frac{L^2 + D_a^2 - D_b^2}{2L}$$

Calculation is simplified somewhat by the fact that L is constant for all stands along a given axis.

When all the stands are located along the x axis, there are stands placed close together which in reality are quite dissimilar. Therefore a second or y axis was constructed to separate these. The first reference stand on the y axis was selected on the basis of the highest e value along the x axis (the stand of poorest fit along the first axis). The value of e is calculated as follows: $e^2 = D_a^2 - x^2$. The other end stand is the most dissimilar one to the first end within a distance from the latter, along the x axis, of less than 10 per cent of the total length of the x axis. In this way the second axis approximates a perpendicular relationship to the first. When the two ends were selected and placed the proper distance apart according to their dissimilarity, the other stands were located along the y axis as they were for the x axis. The stands were then plotted on a two-dimensional graph.

Distances between stands on the ordination were calculated as $d_x^2 + d_y^2$, where d_x is the difference between the two stands along the x axis, and d_y is the difference along the y axis. Correlation between these distances and the respective coefficients of similarity for a random sample of 50 interstand distances was remarkably high ($r = -.922$), indicating that the method yields a close approximation of the relationship of stands to one another based on the coefficients of similarity as calculated above.

Results

Table 1 gives a summary of data for the 60 species recorded. Presence is the number of stands out of 24 in which the species occurred. There are two ubiquitous birds, the Red-eyed Vireo and the Ovenbird. The Black-throated Green Warbler and the American Redstart also show high presence. On the other hand, 15 species (one fourth of the total) were found in only one stand each.

Stand abundance is used here as the average audiovisual density of a species for all stands in which that species actually occurred. It is an indication of the densities commonly reached in the habitat of the species. Highest values are achieved by the Ovenbird and Black-throated Green Warbler; among other widespread species, the Hairy Woodpecker, American Redstart, and Solitary Vireo show low stand abundance. Birds reaching highest audiovisual densities in any stand are the Black-throated Green Warbler, Ovenbird, Red-eyed Vireo, White-throated Sparrow, and Least Flycatcher.

The forest types in Table 1 are rough groupings of the stands studied. The pine "type" includes three stands, one dominated by jack pine, one by red pine, and one by white pine. Because these pine forests are so different from one another, the values in the table are followed by letters indicating in which of the three pine stands the species were found. There were four aspen stands, two almost pure trembling aspen, one trembling aspen mixed with much balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*), and another dominated by big-toothed aspen (*Populus grandidentata*). There were three white birch–red oak stands. The white birch–yellow birch–white cedar type includes six stands, which contain some of all three species, generally with two of the species dominant. There were three hemlock–yellow birch stands. Of the five sugar maple–yellow birch stands two were almost pure maple.

The distribution of stands within the ordination, each identified as to island, is pictured in Fig. 2; they are clustered toward the lower central portion of the graph, with a few scattered stands to the left, the upper left, and the upper right of this concentration. Fig. 3 shows the distribution of 24 bird species within the ordination, and Fig. 4 shows the distribution of certain tree groups and other vegetational characteristics.

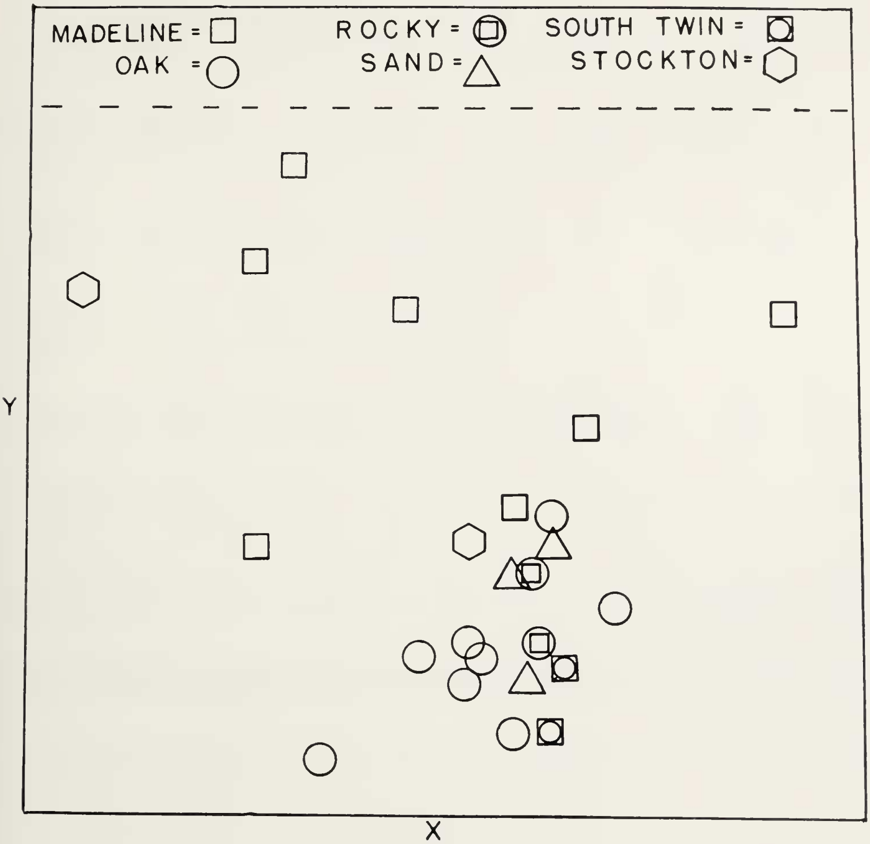

Fig. 2. The distribution of stands within the ordination according to island.

Ecological Distribution of Species

The following observations regarding the ecological requirements or preferences of birds were made. The species are divided into four general groups: those occurring mostly with the Black-throated Green Warbler, those occurring mostly with the White-throated Sparrow, those occurring with both, and those occurring with neither. These two reference species are found in high densities in their respective habitats, and yet their prominence values are negatively correlated with each other, significant at the 5 per cent level. Such a division into groups is quite arbitrary; the divisions were made by simple inspection and not in quantitative terms, but the result is a reasonable grouping of species often found together.

TABLE 1
SUMMARY DATA FOR ALL BIRD SPECIES RECORDED

Species	Stand Presence	Stand Abundance	Maximum Density	Average density for six forest types: Pines*	Aspens	W. Birch–R. Oak	W. Birch–Y. Birch–W. Cedar	Hemlock–Y. Birch	S. Maple–Y. Birch
Goshawk (*Accipiter gentilis*)	1	2.0	2					0.7	
Sharp-shinned Hawk (*Accipiter striatus*)	1	1.0	1			0.3			
Bald Eagle (*Haliaeetus leucocephalus*)	1	2.0	2						0.4
Black-billed Cuckoo (*Coccyzus erythropthalmus*)	1	1.0	1		0.3				
Long-eared Owl (*Asio otus*)	2	1.0	1	0.3^{r}				0.3	
Chimney Swift (*Chaetura pelagica*)	8	2.5	7	0.3^{r}			2.0	1.0	2.0
Yellow-shafted Flicker (*Colaptes auratus*)	8	2.0	5		2.0	1.3			0.2
Pileated Woodpecker (*Dryocopus pileatus*)	3	1.7	3		0.3		0.2		
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	5	2.2	5					3.0	0.4
Hairy Woodpecker (*Dendrocopos villosus*)	13	1.8	5		2.0	0.3	0.8	3.7	0.4
Downy Woodpecker (*Dendrocopos pubescens*)	1	1.0	1		0.3				
Black-backed Three-toed Woodpecker (*Picoïdes arcticus*)	1	1.0	1			0.3			
Great Crested Flycatcher (*Myiarchus crinitus*)	5	1.4	3		0.3	0.3	0.5	0.7	
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	2	3.5	5					2.3	
Traill's Flycatcher (*Empidonax traillii*)	1	3.0	3		0.8				
Least Flycatcher (*Empidonax minimus*)	5	11.6	27		4.5			13.0	0.4
Eastern Wood Pewee (*Contopus virens*)	14	6.9	16	4.3^{rw}	4.0	0.8	2.2	6.3	5.8
Blue Jay (*Cyanocitta cristata*)	15	2.9	8	3.0^{jw}	2.8		1.8	1.0	2.4
Common Raven (*Corvus corax*)	5	1.8	3	0.7^{r}	0.8				0.8
Common Crow (*Corvus brachyrhynchos*)	5	2.8	4	0.7^{w}			0.7		0.4
Black-capped Chickadee (*Parus atricapillus*)	9	3.2	6	0.3^{w}	0.8		1.5	3.3	0.8
White-breasted Nuthatch (*Sitta carolinensis*)	4	3.0	5	1.7^{w}	0.8			1.3	
Red-breasted Nuthatch (*Sitta canadensis*)	4	2.3	4	2.0^{rw}	0.3			0.7	
Brown Creeper (*Certhia familiaris*)	3	1.0	1				0.2	0.3	0.2
House Wren (*Troglodytes aedon*)	2	4.0	5		2.0				
Robin (*Turdus migratorius*)	8	2.4	4	1.3^{jw}	2.0	1.0	0.5	0.3	
Hermit Thrush (*Hylocichla guttata*)	5	3.6	9	3.0^{r}	1.0	1.0	0.2		0.2
Swainson's Thrush (*Hylocichla ustulata*)	15	4.7	10	2.0^{r}	1.8	3.0	4.8	1.3	3.7
Veery (*Hylocichla fuscescens*)	12	3.3	18	0.3^{j}	2.5	9.0		0.3	

* j = jack pine stand, r = red pine stand, w = white pine stand.

TABLE 1 (continued)

Species	Stand Presence	Stand Abundance	Maximum Density	Average density for six forest types: Pines*	Aspens	W. Birch–R. Oak	W. Birch–Y. Birch–W. Cedar	Hemlock–Y. Birch	S. Maple–Y. Birch
Golden-crowned Kinglet (*Regulus satrapa*)	4	1.3	2	1.0^{jw}	0.3			0.8	
Cedar Waxwing (*Bombycilla cedrorum*)	4	3.8	10				1.8	1.3	
Solitary Vireo (*Vireo solitarius*)	16	2.8	10	4.0^{rw}	1.2	1.3	1.0	2.7	2.0
Red-eyed Vireo (*Vireo olivaceus*)	24	17.7	34	10.7^{jrw}	12.8	23.3	23.8	7.3	21.2
Warbling Vireo (*Vireo gilvus*)	1	2.0	2					0.7	
Black-and-white Warbler (*Mniotilta varia*)	14	4.6	10		2.3	6.3	2.7	0.7	3.8
Tennessee Warbler (*Vermivora peregrina*)	1	1.0	1			0.3			
Nashville Warbler (*Vermivora ruficapilla*)	5	2.6	8	4.0^{rw}			0.2		0.4
Parula Warbler (*Parula americana*)	9	3.4	5				3.0	1.3	1.8
Magnolia Warbler (*Dendroica magnolia*)	2	4.0	6		0.5				1.2
Black-throated Blue Warbler (*Dendroica caerulescens*)	4	2.5	4				0.7	0.7	0.8
Black-throated Green Warbler (*Dendroica virens*)	22	21.8	43	16.3^{jrw}	7.8	11.7	29.5	13.3	20.7
Blackburnian Warbler (*Dendroica fusca*)	7	3.7	7	3.3^{rw}			1.3	1.3	0.4
Chestnut-sided Warbler (*Dendroica pensylvanica*)	7	2.6	5		0.3	1.7	1.0		1.5
Pine Warbler (*Dendroica pinus*)	1	4.0	4	1.3^{r}					
Ovenbird (*Seiurus aurocapillus*)	24	23.6	41	24.0^{jrw}	18.8	33.3	19.7	18.3	29.2
Connecticut Warbler (*Oporornis agilis*)	1	1.0	1		0.3				
Mourning Warbler (*Oporornis philadelphia*)	2	12.0	16		6.0				
Yellowthroat (*Geothlypis trichas*)	3	1.7	3		1.0			0.3	
Canada Warbler (*Wilsonia canadensis*)	7	6.1	13			6.0	1.3	4.3	0.8
American Redstart (*Setophaga ruticilla*)	18	2.7	6	3.7^{jrw}	0.5	3.3	2.2	0.3	1.8
Baltimore Oriole (*Icterus galbula*)	2	1.0	1	0.3^{r}	0.3				
Brown-headed Cowbird (*Molothrus ater*)	4	2.3	3		1.3	1.0		0.3	
Scarlet Tanager (*Piranga olivacea*)	6	2.3	4	0.7^{j}		3.0	0.3	1.0	
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	4	1.5	2		0.5		0.2	0.3	0.4
Indigo Bunting (*Passerina cyanea*)	1	1.0	1		0.3				
Purple Finch (*Carpodacus purpureus*)	5	1.8	5	0.3^{r}	0.3		0.8	0.3	0.2
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	1	1.0	1		0.3				
Chipping Sparrow (*Spizella passerina*)	1	2.0	2	0.7^{r}					
White-throated Sparrow (*Zonotrichia albicollis*)	5	15.8	29	1.0^{r}	18.8		0.2		
Song Sparrow (*Melospiza melodia*)	4	6.8	11	1.3^{r}	5.8				

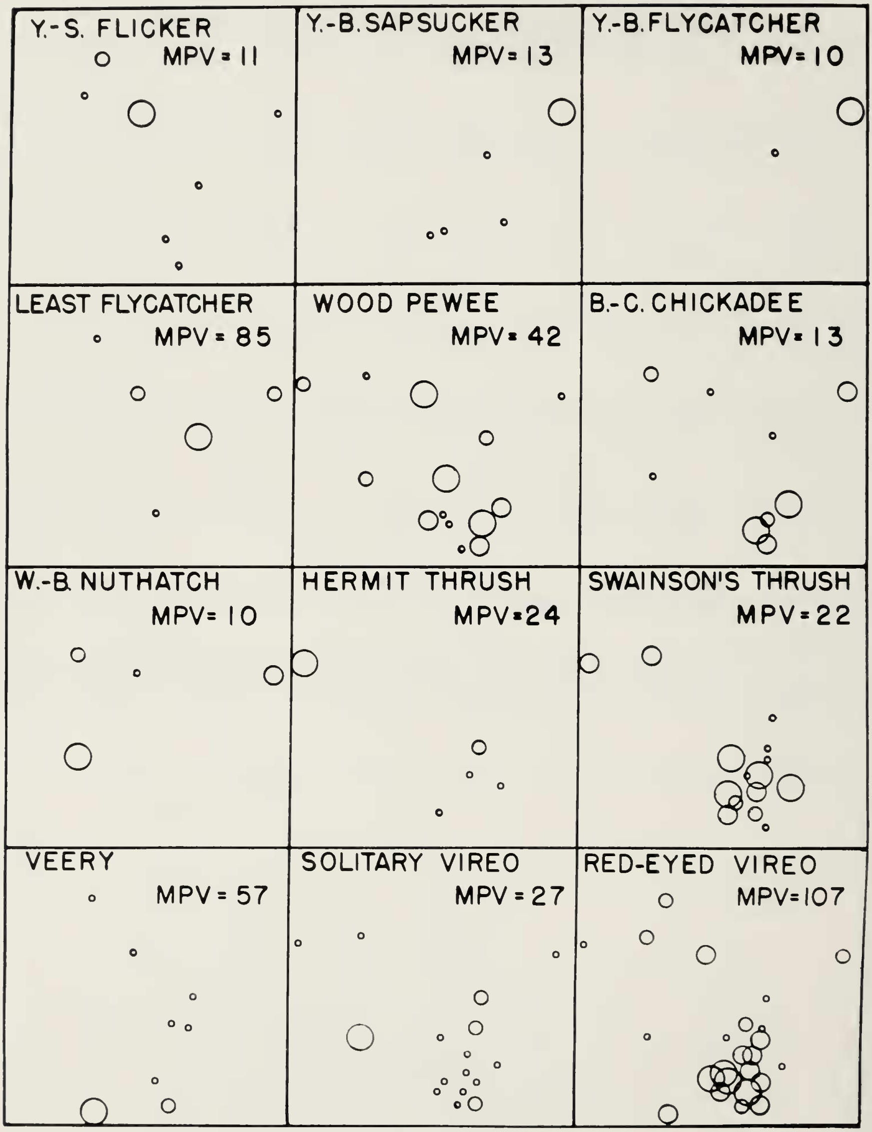

Fig. 3. The distribution of 24 bird species within the ordination. Sizes of circles represent four equal segments of the range of prominence values, based on the maximum prominence value (MPV), of each species.

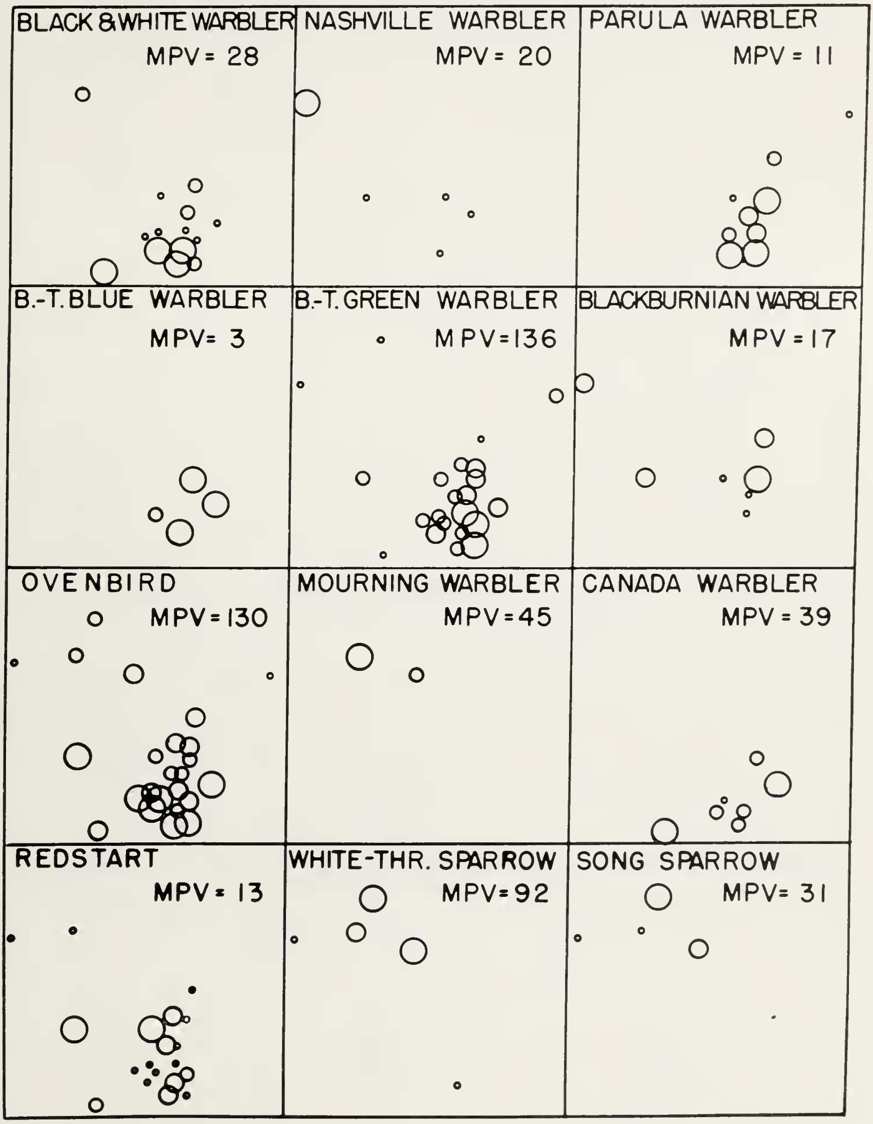

FIG. 3. (Continued)

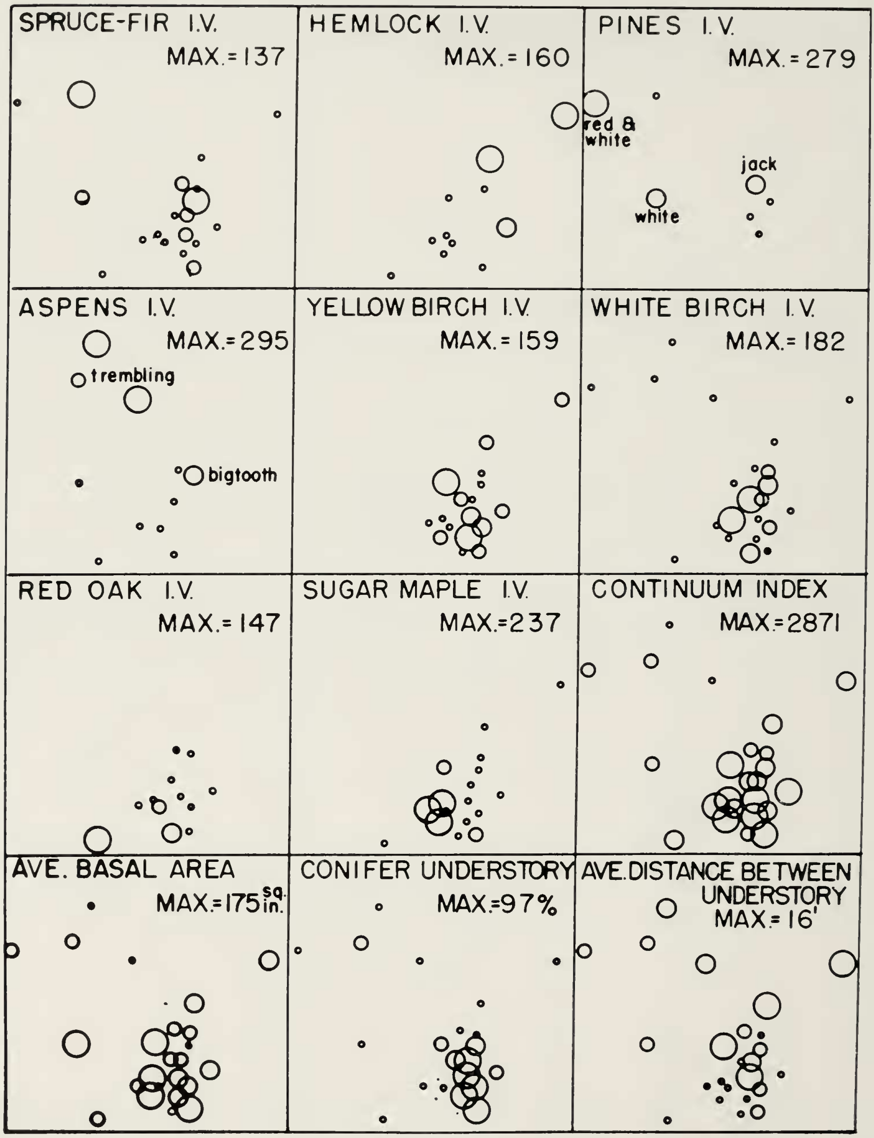

FIG. 4. Distribution of tree species and other vegetational factors within the ordination. Sizes of circles correspond to four equal segments of the range of quantitative values used, based on the maximum value as indicated (I.V. = importance value). For stands where aspens or pines are dominant, the more important species of aspen or pine are named. The dots in the conifer understory block indicate stands with no conifer understory.

Regression was tested in some cases between the species and certain environmental factors. However, most birds respond to a complex of factors, and it seldom happens that a significant value is obtained from an isolated factor. Otherwise the data only suggest trends in the distributions of species. Factors studied were taken from Beals (1958*b*) and included the following: importance values of pines, hemlock, sugar maple, aspens, spruce–fir, white birch, yellow birch, red oak, white cedar, etc.: average basal area of trees, trees per acre, trees at least 10 inches dbh per acre, trees at least 20 inches dbh per acre, total basal area per acre; average distance between stems of woody understory (1 to 7 feet high); relative amount of conifer and understory, etc. One vegetational factor referred to is the continuum index, described for this region by Brown and Curtis (1952). This is based on the importance of trees ranked according to their association with sugar maple at one end and jack pine at the other. A low value (minimum possible, 300) indicates a pioneer forest, and a very high value (maximum possible, 3000) indicates climax vegetation. The values for stands in this study ranged from 614 (aspens) to 2871 (sugar maple forest). See Brown and Curtis (1952) for the method used. This index was tested by correlation coefficient since it is not itself a controlling factor but only an expression of many possible controlling factors.

Birds whose distributions are pictured in Fig. 3 are marked with an asterisk (*) in paragraphs that follow. Those species which occurred in only one or a few stands are mostly just listed, and the reader may refer to Table 1 for vegetational data on them.

Species associated largely with White-throated Sparrow.—The Yellow-shafted Flicker* was widely distributed in small numbers but reached greatest prominence among aspens. This association with aspen coincides with Kendeigh's findings (1948) in lower Michigan and those of Adams (1909) on Isle Royale in northern Lake Superior. Elsewhere it is usually found in relatively pioneer forests also (Odum, 1950; Kendeigh, 1946; Bond, 1957).

House Wrens and Mourning Warblers* were confined to aspen stands, and Yellowthroats were nearly as restricted. Song Sparrows* and White-throated Sparrows* both showed highly significant positive regression with aspen importance values, and a highly significant negative correlation with the continuum index. In other words, these birds all seem to prefer pioneer forests of aspen and to some extent pine. Other studies confirm this preference for pioneer vegetation (Kendeigh, 1946, for Song Sparrow, House Wren, and Yellowthroat; Kendeigh, 1948, for Mourning Warbler and White-throated Sparrow; Stewart and Aldrich, 1949, for Mourning Warbler; and Odum, 1950, for Song Sparrow).

The Veery* was found in greatest numbers in both aspen and red oak forests, especially where understory was densest. In other studies Veeries have been found to be partial to deciduous forest (Kendeigh, 1948; Stewart and Aldrich, 1949). Kendeigh (1945, 1946) reported a preference for late shrub or early tree stages of succession in New York, and McCreary (1909) considered it characteristic of birch–aspen forests on Isle Royale. On the other hand, Odum (1950) found it most abundant in mature oak forest on the highlands of North Carolina. From the present data, both habitats are apparently used in northern Wisconsin.

Additional but uncommon species in this group are the Black-billed Cuckoo, Downy Woodpecker, Traill's Flycatcher, Connecticut Warbler, Indigo Bunting, and Rufous-sided Towhee.

Species associated largely with Black-throated Green Warbler.—The Chimney Swift occurred widely but seemed to prefer forests with many large trees, and with a high continuum index. The Pileated Woodpecker shows some partiality to white cedar. Other workers (Kendeigh, 1946, 1948; Stewart and Aldrich, 1949) have recorded it in mature conifer–hardwoods, and Kendeigh (1948) recorded it also in cedar–fir forest in Michigan. Blackwelder (1909), working in northwest Michigan, reported a preference by this species for edges between fir–cedar swamps and hardwood–hemlock forests. On the other hand, the Yellow-bellied Sapsucker* is found where hemlocks grow, as is the Yellow-bellied Flycatcher.*

Widely distributed in small numbers are the following: the Great Crested Flycatcher, especially where trees are close together; Common Crow; Black-capped Chickadee,* which shows some affinity for yellow birch stands; Solitary Vireo,* which prefers forests with larger trees apparently; and American Redstart,* which reached high densities in two pine stands and one birch–maple stand. The Scarlet Tanager is usually found in fairly dense forests.

The Red-breasted Nuthatch is restricted mostly to pine (except one hemlock stand), and the White-breasted Nuthatch* is also most common in pine and hemlock, with smaller numbers in fir and aspen stands. In Kendeigh's Michigan study (1948) the Redbreast was more common in cedar–fir than in pine, while in New York (Kendeigh, 1946) the Whitebreast showed some preference for mixed forests dominated by hemlock. The Golden-crowned Kinglet was found in stands containing hemlock, fir, and pine. Observations in this study agree with Bent's experience (1949) that this species prefers more open forests with scattered second-growth spruce (or fir) trees.

The Parula Warbler* is found in forests with a rather high continuum index —possibly because more beard moss (*Usnea*), with which it usually constructs its nest, is available in these undisturbed forests, although this lichen is nowhere abundant. This species' association with climax stands was also found by Stewart and Aldrich (1949) in West Virginia and by Odum (1950) in North Carolina, while Kendeigh (1948) found the Parula associated with cedar in lower Michigan.

The Black-throated Blue Warbler* occurred sparsely in hemlock, yellow birch, and sugar maple stands. Odum (1950) and Kendeigh (1946) found this bird most common in stands dominated by hemlock. Others (Griscom *et al.*, 1957) reported that it prefers deciduous trees. No preference one way or the other could be determined from the data of this study. Its usual occurrence where yew (*Taxus canadensis*) forms a part of the understory coincides with the reports of Chapman (1907) and Brewster (1938).

In spite of its rather high prominence in sugar maple stands, the Chestnut-sided Warbler shows a tendency to increase where the size of trees is small or the total basal area per acre is low. Where it does occur with maple, the forests are rather open, with a dense understory (due to selective cutting many years ago of red oak in the stands). It reaches highest densities in stands with large amounts of white birch. Stewart and Aldrich (1949), Kendeigh (1946), and Odum (1950) found it had a strong preference for young deciduous growth, and Odum also found it in mature oak stands opened up by chestnut blight.

The Blackburnian Warbler* increases with the increasing importance of conifers in a forest. This agrees with other reports of this species, except that of Brooks (1936), who said that in West Virginia they are quite at home in deciduous second-growth timber. It is more associated with pine in this study than other observers have found.

The Canada Warbler* shows a definite trend to increase as woody understory also increases, with best development in a red oak woods and in a hemlock stand with much fallen timber. While Kendeigh (1946), Stewart and Aldrich (1949), and Odum (1950) reported it in the more climax vegetation, Brooks (1936) said that it is well adapted to deciduous second-growth in his study area in West Virginia, and Stewart and Aldrich (1952) found it most characteristic of cedar–tamarack–ash bogs in Maine.

The Black-throated Green Warbler* is one of the most common species of the forests, and it shows a positive regression with the importance value of yellow birch, significant at the 5 per cent level. The total importance value of spruce, fir, cedar, and hemlock (all the conifers except pines) also tends to correlate with the prominence of this species. There is a lack of preference for pines, quite contrary to observations in New England (Bent, 1953). Allin (in Griscom *et al.*, 1957) observed a similar scarcity in pines north of Lake Superior. In this study, however, it did occur in moderate numbers where pines were mixed with white cedar or fir. This species shows a strong preference for stands with high conifer composition in most other studies (Kendeigh, 1946, 1948; Stewart and Aldrich, 1949), but Brooks (1940) found it well distributed in northern hardwoods and oak–hickory forests. In the spruce–fir forests on Isle Royale, McCreary (1909) reported this warbler most common where there were many white birch trees among the conifers. In the present study it inhabited areas lacking conifers, but was more common when at least a few conifers (other than pines) were present.

Other species in stands with high values of the Black-throated Green Warbler were the Goshawk, Sharp-shinned Hawk, Bald Eagle, Black-backed Three-toed Woodpecker, Brown Creeper, Cedar Waxwing, Warbling Vireo, Tennessee Warbler, Magnolia Warbler, and Rose-breasted Grosbeak.

Species associated with both reference species.—These included the ubiquitous species and a few others whose environmental requirements, though narrow, apparently cut across those of the two reference species. For instance, the Long-eared Owl was found in a pine stand and a hemlock stand, both of which had some large coniferous trees.

Hairy Woodpeckers were found most prominently in both aspen and hemlock stands but were widely distributed in small numbers, except in the most xeric forests (pine and red oak). In southern Wisconsin Bond (1957) found this woodpecker more common in mesic stands, with sugar maple dominant, than in xeric and intermediate stands, where oaks were dominant. Kendeigh (1948) in Michigan found it in cedar, fir, and aspen types, and other studies (Sutton, 1928; Kendeigh, 1946; Stewart and Aldrich, 1949; Odum, 1950) show it distributed in mesic to wet forests whether pioneer or climax.

The Least Flycatcher* also inhabited aspen and hemlock forests. Two environmental factors were common to the four stands occupied by this bird: very poorly drained soil and mostly deciduous understory. Kendeigh (1948) recorded it in aspen–red maple, cedar–fir, and especially beech–maple–pine woodland.

Wood Pewees* were widely distributed and show little pattern on the ordination. Bond (1957) found a similar lack of patterning in southern Wisconsin for the pewee. With the exception of one aspen stand in which the prominence of this species was high, the size of trees seemed to influence the density of pewees, areas of larger trees being preferred. Kendeigh (1948) in his Michigan studies showed two peaks of population density, one in pine–aspen and one in beech–maple–pine, which correspond somewhat to the results of this study.

Blue Jays and Common Ravens are both scattered over the ordination, and no vegetational characteristics could be pinpointed. Since their territories are rather large, they undoubtedly cover more than one type of habitat.

The Robin is found in aspen, fir, and jack pine forest types, and shows some preference for areas of smaller trees. In Michigan Kendeigh (1948) found it most abundant in pine–aspen, and rather common also in cedar–aspen, cedar–

fir, and aspen–red maple types. Stewart and Aldrich (1949) reported it most common in a young spruce stand. Most observers agree that relatively pioneer vegetation is preferred.

The Hermit Thrush* reached its maximum density in a pine stand, but otherwise was scattered in small numbers in several types of vegetation. Kendeigh's data (1948) indicate that this bird is most common in pine–aspen forest in lower Michigan, with smaller numbers in aspen–red maple.

Swainson's Thrush* is more widely distributed and shows some trend to increase with increasing continuum index values. Stewart and Aldrich (1949) also found this species best developed in climax (virgin spruce–hardwood) forest. The abundance of this species in the Apostle Islands coincides with McCreary's observations (1906) for the near-by Porcupine Mountains in Michigan.

The Black-and-white Warbler* shows preference for the pure sugar maple forests generally. However, its density apparently increases with increasing density of woody understory and with increasing amount of deciduous understory in particular, both of which were characteristic of some of the maple forests studied. In New York Kendeigh (1946) recorded it in all of his three vegetation types, but in Michigan (1948) he found it most common in cedar–aspen and cedar–fir.

The Red-eyed Vireo* and Ovenbird* are two ubiquitous species. The former tends to increase with increasing importance of white birch. Peet (1909) reported that the Red-eyed Vireo prefers white birch forests on Isle Royale. Bond (1957) found Red-eyed Vireo populations densest in the most mesic stands of his xeric to mesic gradient, and in the Apostle Islands white birch occurs most commonly in mesic to wet-mesic stands. The prominence of the Ovenbird shows significant (5 per cent level) regression with the density of the understory, in contrast to Bent's statement (1953) that it usually nests where underbrush is scanty. Stenger (1958) reported that territory size decreased as density of ground vegetation increased in her studies in Ontario. The several nests found in this study were not located in open situations as generally reported (Bent, 1953), but at the base of a tree seedling or among the low branches of a shrub. It was suggested by Stenger (1958) that the understory density is positively correlated with the food supply, which controls, at least in part, population density.

The Baltimore Oriole, Brown-headed Cowbird, and Purple Finch were not very common and showed little pattern within the ordination.

Species not associated with either reference species.—The Nashville Warbler* was most prominent in two of the pine stands, especially the red pine woodland. It also occurred in a cedar stand (as in Kendeigh's findings, 1948) and in two maple–birch stands, one of which contained cedar. Other species found in stands with low densities of the reference species were the Pine Warbler and Chipping Sparrow.

Discussion

Most plants respond to the same group of environmental factors (light, water, mineral nutrients, etc.), though each species responds in a different way from other species. But one animal species may respond to quite different factors from another species. The ground-feeding insectivorous bird is affected greatly by the insects on the forest floor, but it is little affected by the foliage insects; an insectivorous bird of the canopy is affected quite oppositely. Bark-feeders are probably independent of either of these factors, and seed-eaters will be distributed, at least in part, according to still another group of factors.

However, these different factors are all directly or indirectly related to one another. The autotrophic plants form the base of the food pyramid and often furnish nesting sites and materials. These plants, as mentioned before, respond generally to the same environmental factors, each in its own way, and are therefore distributed in some sort of pattern. Thus the animals must also be distributed in a pattern, although it may be more complex and less evident. For an example of interrelation of factors, Stenger (1958) stated that territory size of the Ovenbird increases as canopy density increases. She suggested that density and composition of the canopy influence the density of ground vegetation and the quality and quantity of humus, which in turn determine the abundance of invertebrates in the soil. The Ovenbird feeds upon the invertebrates. Apparently, then, the density of Ovenbirds is determined in part by the indirect influence of the canopy.

Most non-biotic factors, such as water and temperature, influence all animals and therefore also contribute to the patterning. The interaction between and within species must also be considered in the environmental complex. The ordination is constructed to represent this complex of environmental factors, and, if the birds are distributed according to an environmental complex, the more or less distinct patterns formed by most species of birds supports the validity of this representation.

Several species of birds, such as the Chimney Swift, Wood Pewee, Swainson's Thrush, Solitary Vireo, and Magnolia Warbler, do not follow distinct patterns in the two-dimensional ordination, indicating that the environmental complex represented by the ordination is not influencing the distribution of these species markedly. Species of low presence, such as the Magnolia Warbler, may exhibit broad tolerance to the environment expressed in the ordination but have very narrow tolerance to certain environmental characteristics unimportant to the bird populations as a whole. If the species has high presence, as do most of those without distinct distribution patterns, the lack of pattern may reflect a general broad tolerance to environmental variation.

It is important to realize that this ordination gives just one approximation of stand similarities according to the information in the matrix of coefficients of similarity, and that other approximations might be constructed by different criteria and techniques, which would be just as valid, or possibly even more valid. Yet the distances in this ordination and the coefficients of similarity from the matrix do show remarkably high negative correlation ($r = -.922$, for a random sample of 50 interpoint distances out of a total of 276). It would be expected that distances from the four reference stands would be correlated with the respective coefficients; however, most of the 50 sample distances were between stands not used in constructing the ordination. If the coefficients of similarity originally used were valid, and if differences in species composition between stands is an index of environmental differences, the number and importance of environmental factors not included in some way in the framework of this ordination is probably very small.

Certain environmental factors form excellent patterns within the ordination (Fig. 4), suggesting that these are important factors in the distribution of the birds. The distinctive patterns of hemlock, pines, aspens, red oak, sugar maple, and per cent of conifer understory in Fig. 4 give evidence that these factors make important contributions to the habitat. The average size of trees forms a less discernible pattern, but there appear to be areas of large trees and areas of small trees on the ordination, which suggest that tree size is an important modifying factor within the larger environmental framework. The lack of pattern for spruce and fir may reflect the important differences of associated tree species. One of the two stands of high spruce–fir importance had trembling aspen and white pine as codominants, the other had white birch and red maple.

To examine further the ecology of these bird populations, a second ordination of the 24 stands was run based on the vegetation itself. The method was exactly the same, except that the coefficients of similarity were derived from the vegetational data (trees, shrubs, and herbs) rather than from the birds. The coefficients had already been calculated for the report on the vegetation of the region (Beals, 1958*b*). A comparison of the ordination by birds and that by plants is shown in Fig. 5. Groups of stands together in both ordinations were outlined, and each group was labeled by the tree species which was common to the entire group in greatest importance. The similarities are striking, and the differences are enlightening. In the plant ordination the hemlock group is set between the sugar maple and yellow birch groups, indicating that the hemlock stands share many plants in common with the other two groups. Note, however, that the bird populations distinguish the hemlock group as quite different so that it is pushed to one side of this ordination. The special distinctiveness of pine and aspen forests is confirmed by this comparison, since these two groups are much more segregated from the other groups by bird composition than they are by plant composition. The differences between the two ordinations, however, are minor compared with their remarkable similarities, which are good indications of the close relationship between birds and the vegetation.

Furthermore, the general concurrence of the results of this study with those of other investigators in various regions, in regard to vegetation preferences, points up the relatively constant nature of the habitat requirements of most species over their breeding range.

Another biotic factor considered was the effect of deer populations. In spite of the influence of deer on the understory vegetation (Beals, 1958*b*), however, no correlations could be found between the deer pressure (as determined by me) and bird populations.

Geographic factors should also be considered. In Fig. 2 the relation of the islands to the ordination shows definite patterns. In examination of the plant ordination such patterning does not occur, so that vegetation cannot be the cause of the island patterns in Fig. 2. (One exception is Oak Island, the stands on which had a similar grouping on both ordinations. In the plant ordination (Fig. 5) the Oak Island stands include all but one of the sugar maple group, all the red oak group, and the uppermost stand each in the hemlock and fir groups. Their vegetational similarity is probably due to the unique topography of that island, with well-drained, deep soil.)

The Stockton Island maple stand in the bird ordination is pushed toward the Stockton pine stand (Fig. 2), while in regard to vegetation it was quite unrelated, located on the right side of the sugar maple group in Fig. 5, with the pine stand at the extreme left. Also, within the bird ordination the Oak Island hemlock and aspen stands are closer to most of the other Oak Island stands than they are to the other hemlock and aspen stands respectively, although obviously there are indeed great differences in bird populations.

Putting this phenomenon on a quantitative basis, the average coefficient of similarity according to the vegetation was about the same for stands on different islands as it was for stands on the same island (.325 for between-island average, .297 for same-island average), while based on birds the average coefficients for stands on the same islands were higher than the average for stands on different islands (.546 compared with .448). To test the difference, the median test described by Mood (1950) was applied. A distribution-free method was used since the distribution of coefficient values was highly skewed. All coefficients were ranked and the median value found. The number of intra-island values higher and lower than the median, and those for the inter-island values, were set up in a 2×2 contingency table. Chi-square was calculated and was significant at the 5 per cent level. Therefore, local geo-

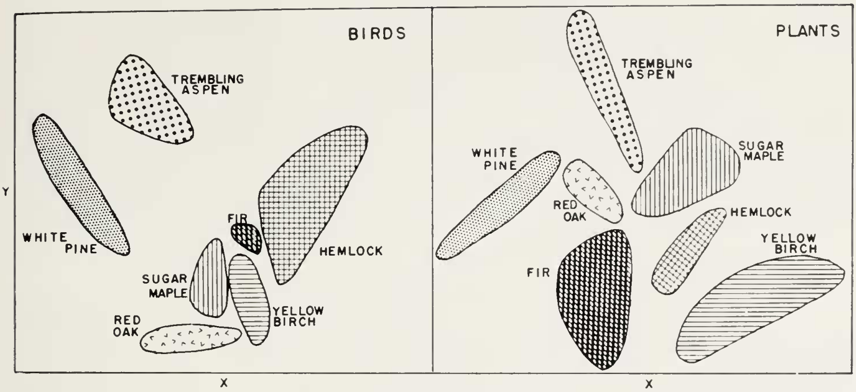

FIG. 5. Comparison of ordination by vegetation and by bird populations. Stands which are grouped together on both ordinations are encircled and are labeled by the tree species which was common to the entire group in greatest importance.

graphic influences apparently do play a role in bird distributions on the Apostle Islands.

The size of islands may have some effect. Fig. 6 shows the relationship of size to the ordination. The two largest islands (Madeline with 13,200 acres and Stockton with 8300) are grouped together. A definite planar gradient can be seen from the smallest island (South Twin, 350 acres) to the next in size (Rocky, 750 acres), to Sand (2900 acres), to Oak (4500 acres), to Stockton and Madeline. Van Tyne (in Hatt *et al.*, 1948) noted that the avifauna on Lake Michigan islands decreased in number of species with decreasing size of the islands, and Lack (1942) reported a similar impoverishment of the bird fauna on small islands around Great Britain. Lack attributes the phenomenon to limitation of habitats, the liability of very small populations of a species to extinction, and the inhibition of migration from other areas by the water. A number of birds in the Apostles were restricted to larger islands (Beals, 1958*a*), such as the birds of prey, Ruby-throated Hummingbird, Yellow-bellied Sapsucker, Yellow-shafted Flicker, Yellow-bellied Flycatcher, Veery, and Baltimore Oriole. Diversity of the bird communities (= diversity of habitats?) is definitely correlated with size of islands: the largest island, Madeline, has the lowest average coefficient of similarity between stands (.402), while each progressively smaller island has increasing average similarity (Stockton, .455; Oak, .621; Sand, .704; Rocky, .773; and South Twin, .849). Furthermore, the larger islands tend to have a greater number of species per individual stand (Madeline, 9–26 species per stand; Stockton, 13–21 species; Oak, 9–20 species) than the smaller islands (Sand, 8–17 species; Rocky, 13–16 species; South Twin, 12–15 species), indicating possible avifaunal limitations

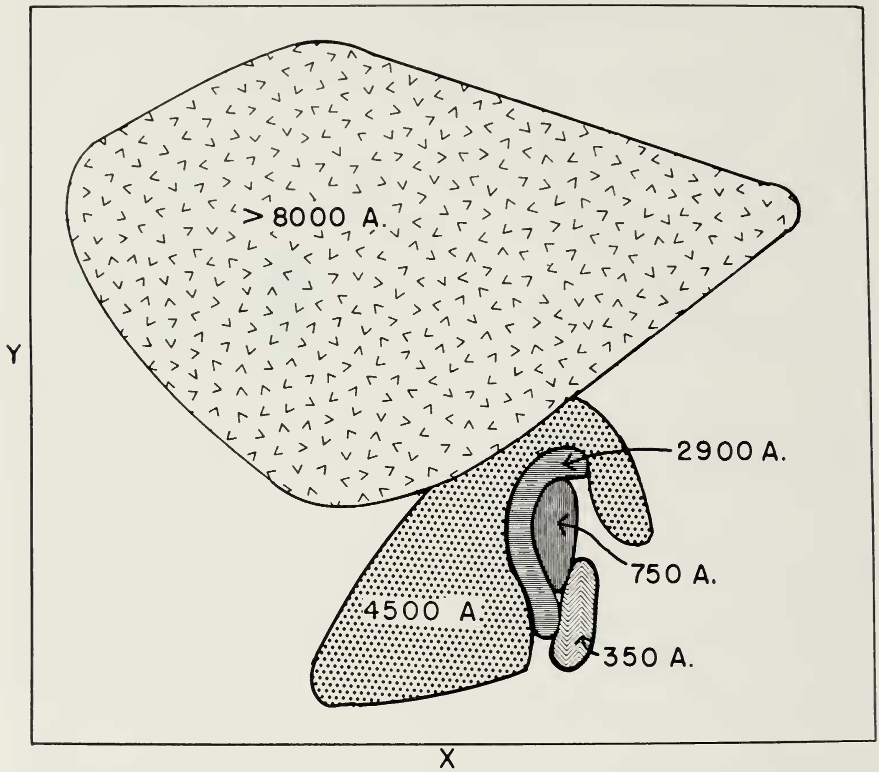

Fig. 6. The pattern of islands in the ordination according to size. Lines surround the stands of an island with the indicated size in acres.

other than lack of habitat variability alone, if one assumes habitat homogeneity in individual stands.

Another geographic influence which may cause added similarity of stands on the same island is related to the behavior of the birds. On the mainland, as population pressure disperses a species into suboptimal environment, individuals may wander considerably until they find suitable habitat, whereas in the island environment large stretches of water (1 to 3 miles or more) may tend to discourage the excess from leaving an island even if all the ideal habitat is occupied. (Unless the birds had some way of knowing that better environment was available beyond the totally unsuitable aquatic habitat, there would probably be little incentive to move out across the water.) Furthermore, the insular topography may accentuate orientation toward the previous breeding or fledging grounds of a bird. This hypothesis would explain the Nashville Warbler's singing in the middle of a birch–maple forest on Stockton, since several hundred yards away was the red pine stand where this species reached its greatest prominence. And the surprising number of Swainson's Thrushes in that pine stand might itself have been an overflow from the near-by woods of more appropriate habitat. Lack (1942) records several instances of modification of habitat on British islands, which were preceded by increased density in the normal breeding habitat. Additional, more subtle associations of populations with islands—perhaps none of which by itself would be considered significant—may combine to give the increased similarity between stands on an island.

Summary

The bird populations of 24 stands of forest vegetation on the Apostle Islands of Lake Superior were censused by a sample count method. A two-dimensional ordination of the stands was constructed, based on the avifaunal similarities between stands. The ordination represents an environmental complex, within which many bird species are distributed in definite patterns. Certain vegetational characteristics of the stands also show well-developed patterns within the ordination, indicating that they may play an important role in the environmental complex. Aspens, pines, hemlocks, maples, and the relative amount of coniferous understory show excellent patterns. The species of birds observed in the study are discussed in relation to their apparent environmental preferences. Two species found in every stand, the Ovenbird and the Red-eyed Vireo, have broad environmental tolerances. Two others found in at least three fourths of the stands, the Black-throated Green Warbler and the American Redstart, are partial to mature forests, the former especially to birch–hemlock, and the latter to pine as well. In pioneer aspen growth, White-throated Sparrows and Mourning Warblers are most abundant. There are greater similarities between stands on the same island than would be expected from the vegetational variation. The possible influences of island size and of the behavior of birds in relation to island topography are discussed.

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